CALATHOSPERMUM FIMBRIATUM SP. NOV., A LOWER CARBONIFEROUS PTERIDOSPERM CUPULE FROM SCOTLAND

by P. D. W. BARNARD

ABSTRACT. A new cupule generically comparable to *Calathospermum scoticum* Walton is described containing ovules identical in form to the seeds known as *Salpingostoma dasu* Gordon. The specimens of this new species illustrate some interesting morphological features new to the genus. The cupule is believed to be equivalent to a large part of a frond and its branching may be interpreted as a pinnate system.

THE material on which these observations are based consisted originally of a block of volcanic ash containing petrified plant remains. It was collected by the late Professor W. T. Gordon. The plants so far described from this source are *Tetrastichia bupatides* Gordon (1938), *Salpingostoma dasu* Gordon (1941), and *Eosperma oxroadense* Barnard (1959). The present communication concerns a large cupule belonging to *Calathospermum* Walton (1940) which is believed to have borne *Salpingostoma dasu* seeds.

The various fragments of the original block of ash, now broken and cut up, have yielded more than ten specimens of this new cupule. Three of these were sectioned by Gordon who prepared thirty-two petrological slides, some of which were lent to Professor J. Walton who at the time was describing *Calathospermum scoticum*. The series, however, did not permit a detailed description, but Walton noted that Gordon's specimens differed from *C. scoticum* in having more divided cupule segments and in having a different vesture. The remaining specimens have been examined by the peel technique of Lacey and others (1956). Rock slices of specimens of *Salpingostoma dasu* not used by Gordon in preparing petrological sections were also examined by the peel technique. Some new specimens of *S. dasu* have also been discovered in the course of these studies.

GENERAL MORPHOLOGY

The cupule is believed to have been borne terminally on the main (primary) rachis of what was probably a special fertile frond (text-fig. 1). Below the cupule the primary rachis, which probably exceeded 7 cm. in length, bore two rows of opposite pinnae at intervals of 10–12 mm. In transverse section the primary rachis is nearly flat adaxially and strongly convex abaxially and measures 6 mm. in width by 3 mm. in height (text-figs. 1, 2A–D). The pinnae on the primary rachis are divided near their base into three portions, possibly the bases of pinnules.

The cupule itself is divided into two halves which may correspond to the two main arms (secondary rachises) typical of many pteridosperm fronds. The base of the cupule would thus be equivalent to the region of bifurcation (text-fig. 1F). Within 3 mm. or so of its origin the secondary rachis gives rise to a pair of lateral pinnae and ends in a terminal pinna (text-fig. 1G). These (primary) pinnae form the basic segments of the cupule.

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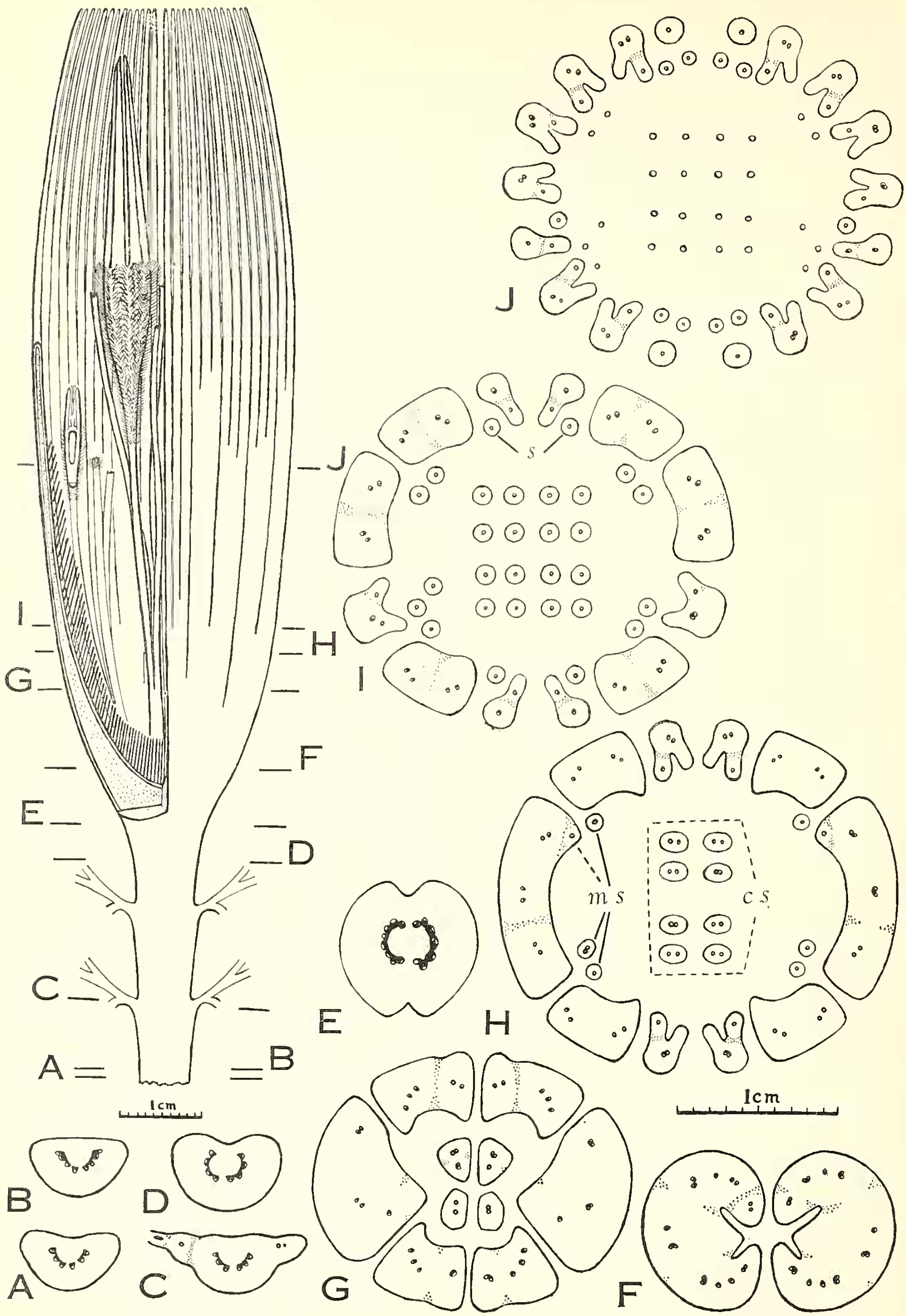

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Each primary pinna or segment bears in turn about five secondary pinnae alternately; of these, the two proximal appear to have been fertile, and the three more distal, vegetative. The rachises of the fertile pinnae may branch dichotomously and may bear from one to four ovules. In *Calathospermum scoticum* the seed stalks (fertile rachises) which arise from a single axis at the base of the cupule were called collectively the central (stalk) system by Walton. This term is used here for the rachises of the four fertile pinnae which arise from the bases of the lateral primary pinnae. The marginal system in *C. scoticum* is here represented by the remaining fertile pinnae. The sterile secondary pinnae branch in an alternate manner and end in from three to five or sometimes more ultimate, uninerved, cylindrical processes (pinnules) which I have called strands (*s* in text-figs. 1, 3). As shown in the reconstruction (text-fig. 1), some of these strands exceed 5 cm. in length and have an average diameter of 1 mm. The tip of the cupule was not preserved in any of the specimens examined so that the exact total length is uncertain. In all but one of the specimens examined the rachises of both the central and marginal systems as traced upwards become poorly preserved and shrunken in appearance and apparently end some 2 to 3 cm. above their origin.

Recognizable attached ovules, two of which are shown in (text-fig. 3C, D), have only been seen in one specimen (no. 2); this contained at least three and probably four small, poorly preserved ovules. Two of them belonging to the marginal system are borne terminally on the undivided rachises of fertile pinnae. One of these (text-fig. 3C) arises from the abaxial margin of the terminal pinna and the other from a lateral pinna. The stalk of the third ovule (text-fig. 3D) had its origin on the left abaxial lateral pinna, and separated from it at a level in between that of the lowest fertile pinna rachis and that of the first strand (*a* in text-fig. 3A). It does not appear to have affected either of the two 'branches' between which it is interpolated.

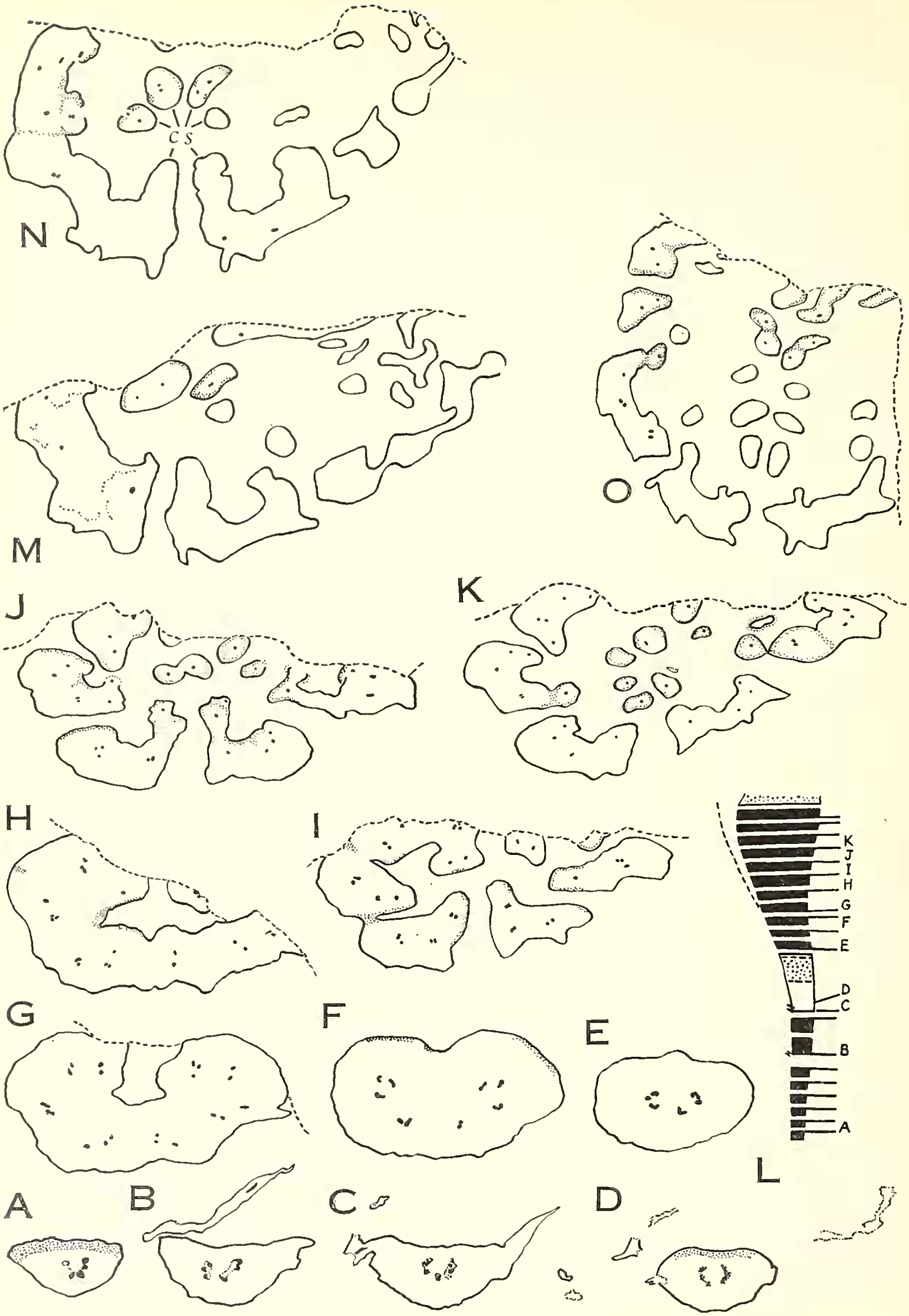
ANATOMY

The epidermis. As seen in surface sections of the rachis the epidermal cells are mainly rectangular, though some have an inclined end wall, and others are five-sided with a gable end. When seen in transverse section they appear nearly square, and in radial longitudinal section, rectangular. The average dimensions are: length, 102 μ; radial height, 34 μ; tangential width, 38 μ. Stomata appear to be present on the primary rachis (text-fig. 4A, B). They may also have been present on the outside of the cupule lobes.

In the lowest 3 cm. of the cupule, large epidermal hairs with an average diameter of 45 μ are found on the inside of the segments and their subdivisions. They are very long, straight, and without apparent cross walls. I estimate that they were at least 5 mm. long and may even have exceeded 10 mm.

Fine epidermal hairs, with an average diameter of 13 μ, are present around a few of the seed stalks and also around the ovules in specimen 2 (text-fig. 3B; Pl. 45, fig. 5).

TEXT-FIG. 1. *Calathospermum fimbriatum* sp. nov. Reconstruction of the frond with a quarter of the cupule cut away to reveal the contents; the fertile rachises, one bearing an ovule shown in section and another a *Salpingostoma* seed; together with transverse sections A to J through the regions indicated. In section H, *ms*, the fertile rachises of the marginal system (on the left only); the fertile rachises of the central system are inclosed —*cs*—. In section I, *s*, strand.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Similar hairs occur in *Salpingostoma dasu*, where they are found on the body of the seed and on its stalk, but only for some 5 to 10 mm. below the base of the seed.

The cortex. This is differentiated into two distinct zones, an inner parenchymatous ground tissue, and an outer fibrous zone or sterome.

The sterome is composed of a number of rows of longitudinally elongate cells of small diameter and fairly thick walls. The average dimensions are: length, 500 μ+; diameter, 33 μ; wall thickness, 4 μ. The sterome is broken radially by numerous gaps with such an irregular disposition that it cannot be called a 'sparganum'. Some of these gaps appear to underlie stomata in the epidermis.

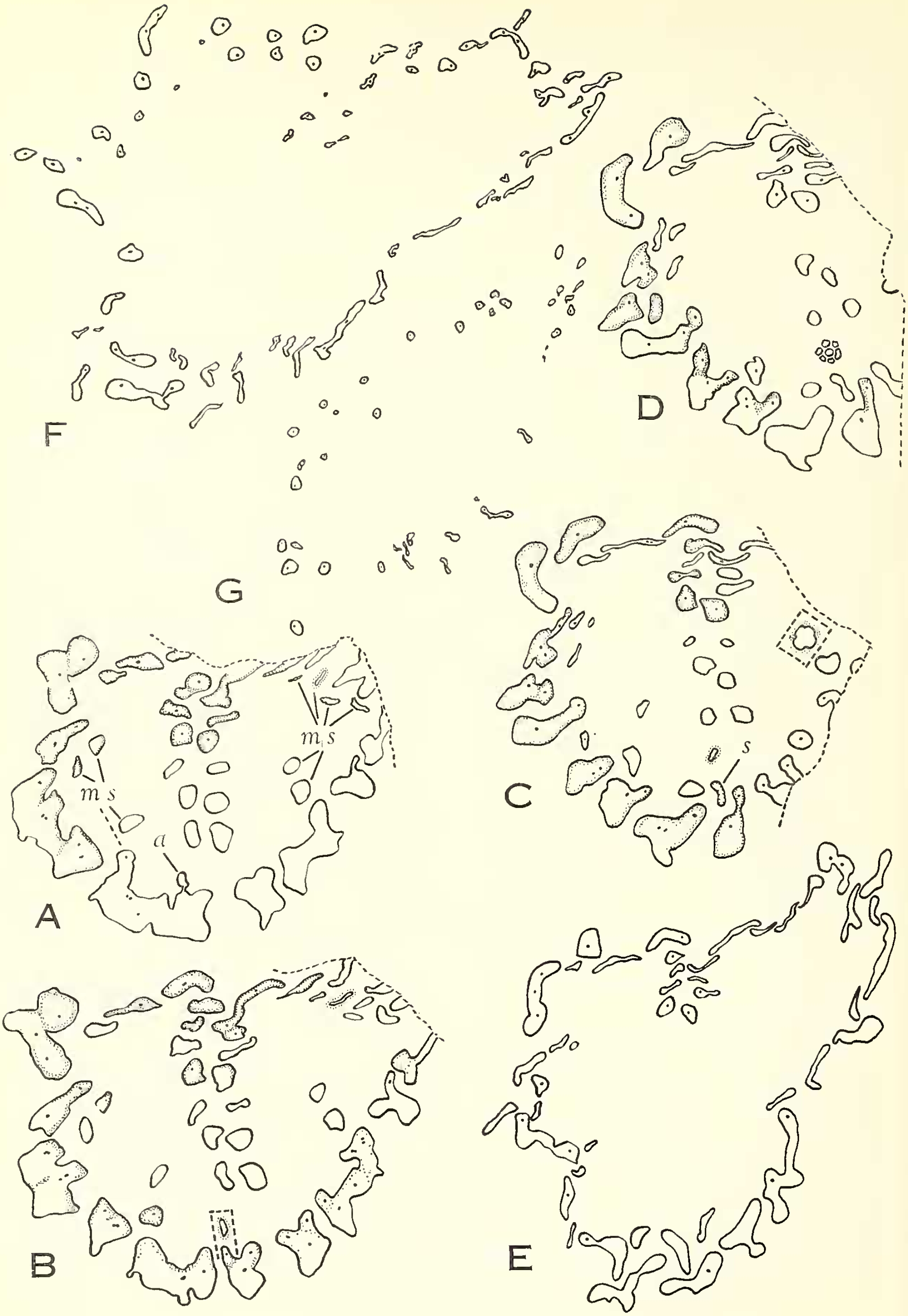
The distribution of the fibres is probably related to the mechanics of the cupule: thus in the primary rachis the sterome is generally better developed abaxially than adaxially; it is greatly reduced in the conical base of the cupule, but increases again all round after the primary division into segments, only to decrease again in the pinnules. The sterome thickens in the base of the seeds as indicated by Gordon.

The ground tissue consists of large empty isodiametric parenchyma cells about 100 μ in diameter, amongst which are scattered slightly larger 'secretory' cells with black, often crystalline contents, and nests of somewhat similar cells which are surrounded by clear parenchyma cells which are somewhat radially elongate with respect to the centre of the nest. These nests of dark cells occur very regularly in the adaxial groove in the xylem of the primary rachis, and give a scalariform appearance to longitudinal sections, but elsewhere their distribution is more random.

The vascular system. The xylem of the vascular bundles is often extremely well preserved whilst the phloem cannot be discerned, but it may be represented by part or all of the cavity surrounding the xylem. The xylem is mesarch and consists of annular protoxylem tracheids, reticulate to pitted centrifugal tracheids, and pitted centripetal tracheids (text-fig. 4C and D), with pits about 7 μ in diameter, distant and the pit apertures horizontal and opposite. The tracheids range in diameter from 14 μ (protoxylem) to 40 μ (metaxylem).

In the primary rachis the bundle was probably a continuous U-shaped strand, though as seen now it is always irregularly broken especially at the bottom. The xylem contains from 6 to 8 protoxylem groups, one situated in each of the abaxial ridges of the strand. The most abaxial pair of protoxylem groups divide just above the 'pinna node' and the new groups so produced depart from the central bundle to form separate traces which run parallel to the parent bundle until they pass into the pinnae at the next 'node'. As they pass out they divide to form two xylems of unequal size, the larger of which soon divides again.

TEXT-FIG. 2. *Calathospermum fimbriatum* sp. nov. A–K, Series of transverse sections (specimen 1) showing the origin of the lateral pinnae on the primary rachis, and the basal segmentation of the cupule. Owing to the slightly oblique nature of the sections the fertile rachises of the central system depart from the adaxial primary pinnae between I/J and the abaxial primary pinnae between J/K. A, G.C. 2190; B, G.C. 2196; C, G.C. 2198; D, G.C. 2203 (peel 23); E, G.C. 2207; F, G.C. 2209; G, G.C. 2210; H, G.C. 2211; I, G.C. 2212; J, G.C. 2213; K, G.C. 2214; L, restored outline of the same specimen to show the position of the petrological sections and the small portion peeled. The letters A to K indicate the sections illustrated. M to O, basal sections of a series of oblique transverse sections (specimen 2) continued in text-fig. 3. In N, *cs*, fertile rachises of the central system. Owing to the oblique nature of the section the adaxial rachises are shown above their first division whilst abaxially they are still attached. M, G.C. 2218; N, G.C. 2221; O, 2223. All $\times 3$, except L $\times 1$.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As the primary rachis enlarges into the base of the cupule the strand divides to give two C-shaped portions, each of which then breaks up into three; its further subdivisions follow those of the cupule. Each division of the xylem occurs at a distance of from 5 to 15 mm. below that at which the individual parts of the cupule they supply become free from one another. The strands and the fertile rachises contain a single oval xylem bundle with an excentric mesarch protoxylem. Re-examination of the stalks of *Salpingostoma dasu* revealed a single oval xylem bundle in three specimens. This is shown in Gordon's pl. 1, fig. 6, but it is rather obscured in that specimen by the pyrite. The single oval bundle when traced upwards into the seed becomes horseshoe-shaped (Gordon's term) before dividing to produce the six oval integumentary bundles.

CORRELATION WITH *SALPINGOSTOMA*

There are three reasons for relating the seed *Salpingostoma dasu* to this cupule: the discovery of small ovules in some of the cupules, the presence of fine hairs in some of the other cupules, and the close histological similarity.

The best ovule is shown in text-fig. 3D, where one can clearly see the apical processes. Unfortunately the body of this ovule was lost in the preparation of petrological sections. Its stalk, surrounded by a belt of fine hairs, is shown in Pl. 45, fig. 5.

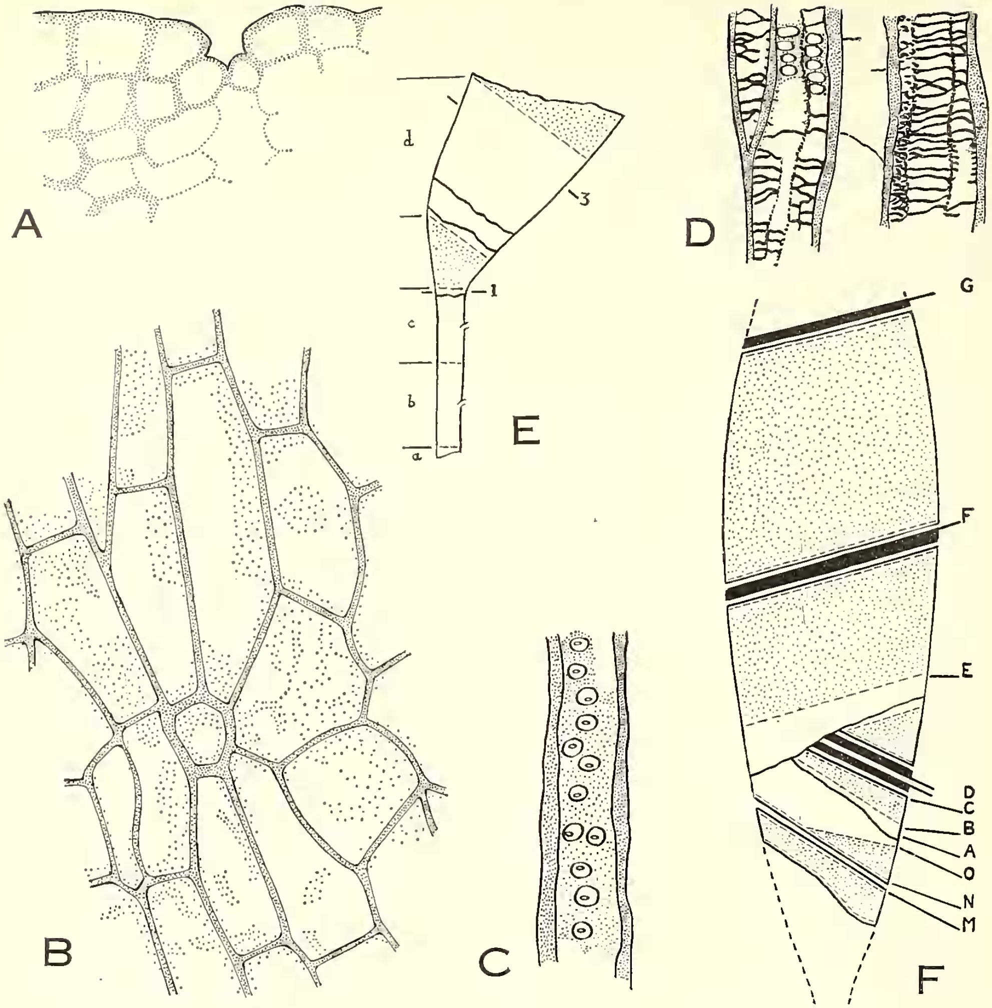
When traced upwards the seed stalks in the cupules become collapsed and poorly preserved just before they disappear. The stalks of *Salpingostoma* seeds fade out similarly downwards. I believe that rupture of the stalks was not confined to a specialized abscission zone, but rather that it occurred at any weak point. Most of them appear to have parted in the hairless region, but an occasional one broke slightly higher so as to leave part of the hairy region in the cupule.

The approximate dimensions of the ovules is shown in the table alongside those of *C. scoticum* and *S. dasu* after Walton (1949).

	Salpingostoma	*Calathospermum*	
	dasu	*C. fimbriatum*	*C. scoticum*
Number of tentacles	6	6	9+
Length of ovular body	14 mm.	3·5 mm.	3 mm.
,, ,, tentacles	25 mm.	4 mm.+	12 mm.
Diameter of ovular body	6 mm.	1·2 mm.	1·9 mm.
,, ,, tentacles	1·2 mm.	0·25 mm.	0·21–0·25 mm.
,, ,, lagenostome	1·6 mm.	0·6 mm.	1·4 mm.
,, ,, salpinx	0·4 mm.	0·3 mm.	0·47 mm.
,, ,, hairs	12–20 μ	10–15 μ	12–14 μ

That the size differences may be due to differences in maturity was mentioned by Walton. In this instance it would appear probable that the ovules were abortive and

TEXT-FIG. 3. *Calathospermum fimbriatum* sp. nov. A–G, Continuation of the series of oblique transverse sections (specimen 2) commencing in text-fig. 2M. A, Showing *a*, the anomalous departure of the stalk of an ovule from the left abaxial primary pinna (segment); *ms*, fertile rachises of the marginal system. G.C. 2225. B, The first vegetative secondary pinna has now separated from the left abaxial segment. The ovule stalk surrounded by the interrupted line is shown in Pl. 45, fig. 5. G.C. 2229. C, Showing the body of an ovule of the marginal system sectioned medinally; it is illustrated again in Pl. 45, fig. 6. The left abaxial segment is now represented by three secondary pinnae, from one of these a strand *s* has separated. G.C. 2235. D, Petrological section showing the six tentacles and lagenostome of the ovule with the anomalous stalk attachment. G.C. 2236. E, G.C. 2245. G, G.C. 2248. All ×3.



TEXT-FIG. 4. *Calathospermum fimbriatum* sp. nov. A, Transverse section of primary rachis showing epidermis with probable stoma and a portion of the sterome. G.C. 2282 (peel 6), ×250. B, Surface section of primary rachis showing epidermis with probable stomatal pit. G.C. 2283 (peel 1), ×250. C, Radial longitudinal section of pitted centripetal tracheid. G.C. 2286 (peel 57), ×300. D, Radial longitudinal section of reticulate to pitted centrifugal tracheids. G.C. 2285 (peel 52), ×300. E, Restored outline of holotype to show extent of specimen and regions peeled, unpeeled portion stippled; transverse series *a*, 10 peels; *c*, 60 peels and *d*, 88 peels; *b*, longitudinal series of 100 peels. 1 and 3 indicate positions of sections illustrated in Pl. 45, figs. 1, 3, ×1. F, Restored outline of specimen 2 to show the positions of the petrological sections, regions peeled, and the positions of the sections in text-figs. 2, 3, ×1.

that the mature seeds had been shed. A few small detached seeds the same size as the ovules in the cupule have been discovered in the course of this investigation. It is possible that these could be the seeds of this cupule and *S. dasu* the seeds of a different and possibly larger cupule. One of these new seeds contained microspores (? pollen) in its lagenostome (Pl. 45, fig. 7). Large quantities of similar microspores, many of them still adhering in tetrads and in larger masses, are present in cupule specimens 2 and 3. The single seed found containing microspores might, therefore, represent a post-pollination stage ovule which became detached preventing further development.

The histology of *S. dasu* differs from that of the cupule in only two minor details. The xylem in *Salpingostoma* was only observed to consist of annular and reticulate (scalariform) tracheids, whereas in the cupule rachis pitted forms were also present. The megaspore membrane of *S. dasu* as revealed by maceration of a small portion of Gordon's seed no. 8 (Pl. 45, fig. 8) is similar to that found in one of the new small seeds, except that the fibrils of the membrane are more widely separated (expanded) and the meshes of the cellular reticulum on the outer surface are approximately 350 μ as compared to 250 μ in the smaller seed.

Genus CALATHOSPERMUM Walton 1940

Emended diagnosis. Cupule borne terminally on a dorsiventral rachis and containing numerous stalked ovules. Cupule consisting of six main segments which may be simple or divided. Ovules borne terminally on rachises which arise marginally on the segments or from the base of the cupule or from both. Ovules similar to the seeds of the type known as *Salpingostoma* Gordon 1941.

Calathospermum fimbriatum sp. nov.

Plate 45, figs. 1–7

Cupule about 90 mm. long and 30 mm. broad at its widest part, borne on a primary rachis 6 by 3 mm. in diameter. Cupule bilaterally symmetrical and divided into equal halves from just above the base, each half again divided into three segments. Each segment subdivided into five pinnae, the two basal of which are seed-bearing, and the three higher sterile. Fertile pinna rachises with from one to four ovules. Sterile pinnae ending in three or more strands, 1 mm. in diameter.

Material. Holotype specimen no. 5, slide nos. 2279 to 2330; Gordon collection, Geology Department, King's College, London: and paratypes slides nos. 2190 to 2385; together with peel collection and rock specimens from the Green Ash within the Cementstone Group (Upper Tournaisian) of the Calciferous Sandstone Series (Lower Carboniferous) at Oxroad Bay, in East Lothian, Scotland.

Discussion. The view adopted here that *C. fimbriatum* is a modified frond is the one advanced by Walton in 1949. This appears fully justified by the morphology and anatomy of the cupule stalk in *C. fimbriatum* which is unquestionably a rachis. If only an isolated portion of such a stalk had been found (e.g. Pl. 45, fig. 2) it would have been described as a rachis and placed in the form genus *Lyginorachis*.

Some light may be thrown on the question as to whether the stalk is a primary or secondary rachis by comparison with *Lyginopteris oldhamia* (Binney) as described by C. Louvel (1959), and *Tetrastichia bupatides* Gordon (1938). In *L. oldhamia* the primary rachis (petiole) bears opposite pinnae and above the bifurcation the secondary rachises bear alternate pinnae. The primary rachis contains a W-shaped xylem strand formed by the partial fusion of two V-shaped traces which supply the secondary rachises. In *T. bupatides* there are no pinnae on the petiole (primary rachis); on the secondary rachises the pinnae are alternate (original observation). In the petiole the xylem strand is butterfly shaped (a modified W) and separates into two modified V-shaped traces at the bifurcation.

In comparing the two species of *Calathospermum* a number of differences become apparent. The cupule segments in *C. scoticum* are not pinnately divided yet they contain six xylem strands. The seed-bearing branches of the central system in *C. scoticum* arise from a central stalk which appears as a direct continuation of the primary rachis (cupule stalk), and the marginal system is more extensively developed in that twelve pinnae contribute to it as opposed to the eight in *C. fimbriatum*. The four extra pinnae in *C. scoticum* arise from the lateral pinnae (cupule segments). In *C. fimbriatum* (specimen 2) the ovule which arises in an anomalous position appears to be a homologue of one of the extra marginal pinnae in *C. scoticum*.

The two cupules also differ markedly in their relative proportions. The cupule of *C. fimbriatum* is twice as long as that of *C. scoticum* and the diameters of their stalks are in the same proportion. However, the diameters of the two cupules are about equal. The fertile rachises in *C. fimbriatum* arise over a distance of about 9 mm., whereas in *C. scoticum* they all arise within 3 mm. of one another. These proportional differences suggest the following explanation for some of the morphological differences: that the number of fertile pinnae per cupule is determined by some factor correlated with growth in diameter, and that the basal origin of the central system in *C. scoticum* is due to a telescoping of the region over which the fertile pinnae arise.

Walton (1949) has compared *C. scoticum* and *Diplopteridium tielianum* (Kidston) Walton. It is interesting to note that the frond of *C. fimbriatum* appears to be intermediate between *D. tielianum* and *C. scoticum* in having pinnate cupule segments. The fact that *C. fimbriatum* is basically pinnately branched contrasts strongly with *D. tielianum* where the fertile rachises arise as a direct continuation of the primary rachis.

Walton (1949), in a very full discussion, compared *Calathospermum* with *Gnetopsis elliptica* Renault, *Megatheca thomasii* Andrews, *Calathiops renieri* Walton, and *Calathiops bernhardti* Benson. The first three of these species are only known as detached

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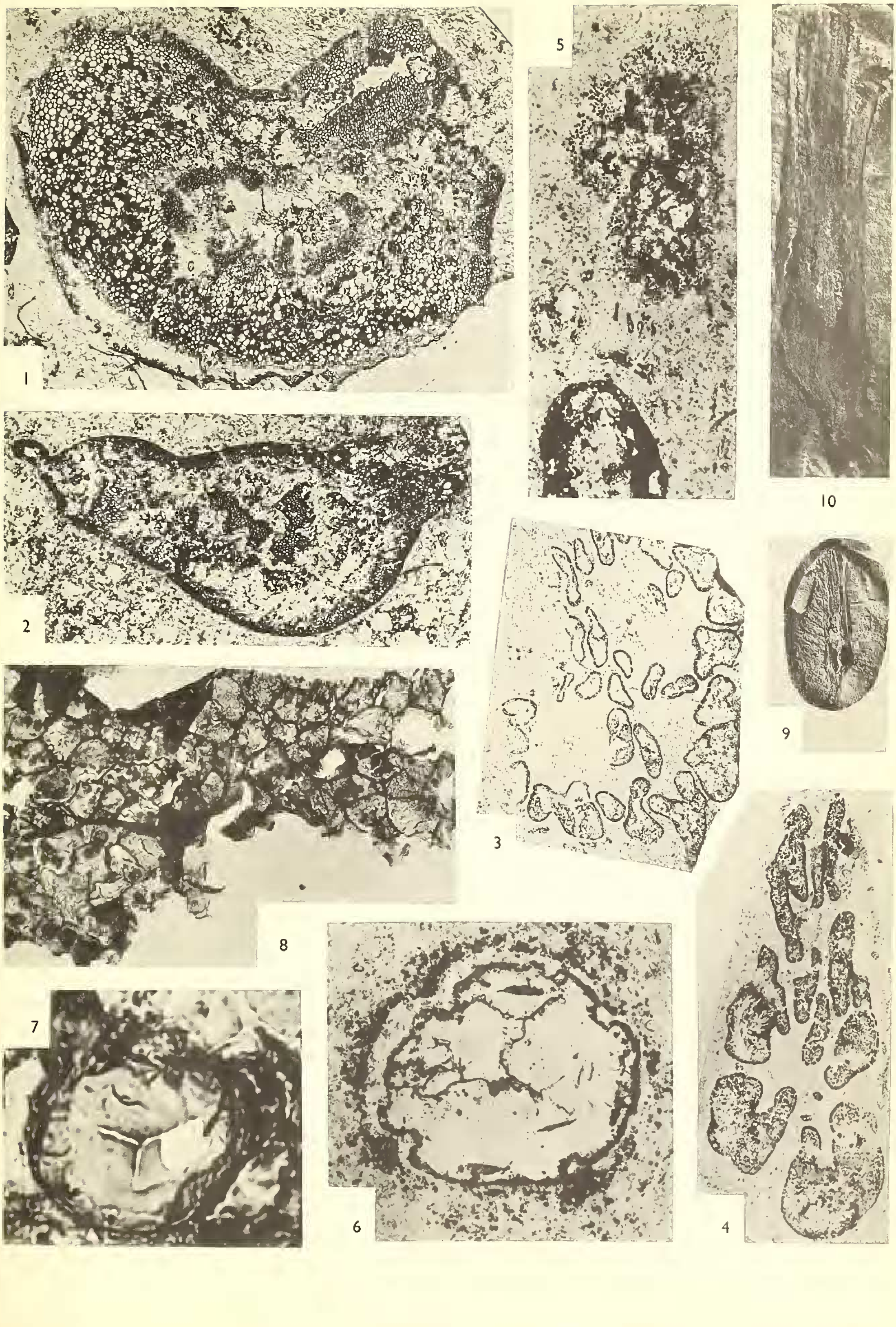
EXPLANATION OF PLATE 45

Figs. 1–7. *Calathospermum fimbriatum* sp. nov. 1, Transverse section of primary rachis containing two dividing C-shaped traces from the extreme base of the cupule; holotype, slide no. G.C. 2296 (peel 3), ×13·5. 2, Transverse section (oblique 30°) of a small detached rachis (*Lyginorachis sp.*?) identical in structure to a primary rachis of *C. fimbriatum* and showing the characteristic broken dentate U-shaped xylem and the bases of two pinnae; G.C. 2378, ×13·5. 3, Transverse section through the holotype showing eight rachises of the central system, together with six rachises of the marginal system surrounded by the cupule segments in various stages of division (compare with text-fig. 1H and I); G.C. 2324, ×3·5. 4, Oblique transverse section showing six segments and centrally two fertile pinna rachises; specimen 6, G.C. 2342, ×3·5. 5, Transverse section of the stalk of an ovule surrounded by hairs (text-fig. 3B); G.C. 2229, ×36. 6, Transverse section through the body of an ovule (text-fig. 3C), showing the crumpled megaspore membrane, superficial layers of integument with five grooves and surrounding hairs; G.C. 2234, ×38. 7, Microspore (?pollen) from lagenostome of small detached ovule; G.C. 2384 (peel 10), ×666.

Fig. 8. *Salpingostoma dasu*, portion of megaspore membrane showing the cellular reticulum on the outer surface; G.C. 2383, ×21.

Figs. 9, 10. *Calathiops sp.* W. Hemingway's photographs of a specimen from Coseley. 9, Specimen in nodule, ×1. 10, Counterpart, ×3.



BARNARD, *Calathospermum*